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DORMANCY AND HARDINESS IN THE PLUM

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(WITH FOUR FIGURES)

It is a well known fact that the trees of our latitude develop buds during the period of vegetative activity, which remain inactive or dormant throughout the succeeding period of climatic conditions unfavorable for growth and development (ASKENASY 1). Although these dormant structures have been recognized for a long time, practically nothing is known concerning the factors involved in their development or the internal conditions that obtain during the time of their relative inactivity. Growth and development take place normally up to a certain point and then suddenly cease, in some instances several weeks earlier than the occurrence of temperatures sufficiently low to arrest growth activity. In late winter, the rest period is broken in many species, and growth changes are manifested long before the incipiency of warmer weather. Up to the present no specific experiments have dealt with the nature of the forces that induce cessation of growth in these bud structures, or the changes involved, either internal or external, in the resumption of the activity after a certain period of rest. The term "rest" as used here refers to a condition of greatly reduced, or possibly (for very short periods under certain conditions) a complete arrest of growth activity. Although no growth effects

are visible during dormancy, the metabolic processes are probably continued most of the time at a very greatly retarded rate.

In the plum there is a very definite relation between dormancy and hardiness or the ability to withstand low temperatures without suffering injury. Different species and varieties manifest widely differing degrees of dormancy, and in general the more profound the dormancy, the greater is the degree of hardiness. Furthermore, there is a close correlation in the plum between early maturity and deep dormancy, because those forms which show evidence of the earliest maturation in autumn are likewise the ones possessing the greatest degree of dormancy. This is a very significant relationship, for according to CHANDLER (4) maturity is "the most important factor affecting the hardiness of plant tissue."

Dormancy in seeds has been studied quite extensively, but little has been done to ascertain the nature of the dormancy that occurs in buds. The literature extant deals largely with the possible effects that external factors and forcing agents may have upon the rest period. SCHIMPER (10) maintains that "the protoplasm of the plants of temperate zones exists in two conditions, one active and one quiescent, and that the regular periodic alternation of these conditions is occasioned by inherent hereditary characters." HOWARD (6) asserts that "the rest sets in on account of the inhibition of enzymic activity due to over-accumulation of the products of their work." He holds that respiration and enzyme activity, continuing at a reduced rate, gradually remove the surplus of accumulated carbohydrates, and as a result the condition of dormancy is gradually lost. He further states that the fact "that the main dormant period happens to be coincident with the winter season is doubtless a mere coincidence, as the winter per se may, and probably does, have nothing to do with the beginning of the rest." This coincidence in all probability has a deeper significance than that which appears in this brief statement. Dormancy, whatever it involves, certainly represents an accumulation of tendencies which have been occasioned in the experience of the plant by marked changes in its environmental relations. Within the history of the plant kingdom striking temperature changes have occurred, and those forms which failed in the development of a

dormant condition, capable of resisting low temperatures, were eliminated from the field, and the forms which became dormant survived. Thus this coincidence is a direct result of adaptive reactions which have become a part of the heritage of the species. KLEBS (8) succeeded in preventing dormancy by controlling culture conditions, and MOLISCH (9) could break dormancy at will by subjecting the twigs to a water bath at high temperatures for a period of 10–12 hours.

While the knowledge of the external factors which affect dormancy gives a clearer comprehension of the phenomenon, an intensive chemical and physiological study of the changes in the bud at all stages in the growth cycle are required to discover the internal changes which parallel or precede the visible external changes. From such studies only can the facts be obtained which are essential to a full understanding of the changes that induce the rest period, the conditions that obtain during dormancy, or the initial changes in the resumption of growth.

Accordingly this investigation was begun with the object of determining some of the conditions which prevail in plum buds during the dormant period. Chief attention has been given to differences in the degree of dormancy in certain hardy and semi-hardy varieties, and to determining what relation (if any) might exist between the moisture content or moisture retention of dormant buds in different species and the relative resistance of these buds to low temperatures.

Material and methods

All the material used in this investigation was obtained from the University of Minnesota Fruit Breeding Farm at Zumbra Heights. Three varieties differing in hardiness were selected for study. The hardiest form, Assiniboine, is a variety of *Prunus nigra*, and has suffered little if any bud injury in Minnesota, even during the severest winters. Tonka is a cross between *P. triflora* var. Burbank and *P. americana* var. Wolf. The other variety, Stella, which has been used extensively, like Tonka, is a cross between *P. triflora* and *P. americana*. These two varieties differ markedly from Assiniboine in that during the most severe winters

as many as 50 per cent of the flower buds may be killed; consequently they may be placed in the semihardy group for a considerable portion of the state. The trees of each of these varieties from which material was obtained are about eight years old, and are growing in a dark, rich, silt loam soil. All are under clean cultivation without cover crops.

In making the moisture determinations, fruit buds were collected at the Fruit Breeding Farm in glass weighing dishes provided with closely fitted covers, at intervals varying from one to two weeks during the months from November 2 to March 31. On the evening of the same day the dishes containing the buds were brought into the laboratory, carefully weighed, and placed in an electric vacuum oven at 95°–98° C., with the pressure reduced to 8.5 cm. of mercury. The buds were kept in the oven until successive weighings indicated that all of the water had been removed from the tissues. In all determinations made before the middle of January it required about 72 hours to bring the buds to constant weight. After this date the desiccation began to take place more rapidly, and during the latter part of February the moisture could be completely evaporated in 24 hours. The extremely small size of the buds made it practically impossible to secure large samples for these determinations, since 200–250 buds were required for a single gram, wet weight. In the dehydration experiments the usual method was followed, in which the buds or twigs were placed in sealed chambers over sulphuric acid.

Relative degree of dormancy in hardy and semihardy forms

In determining differences in the degree of dormancy between the hardy and semihardy varieties, twigs were cut at intervals between October 3 and March 5 inclusive, and placed in water in the laboratory or greenhouse. In this way the fruit and flower buds were exposed to ordinary room temperatures, and careful notice was taken of all visible changes undergone, as well as the time required for anthesis. The results of these studies are shown in table I.

It is quite evident from these data that the buds of the semihardy varieties possess a very light dormancy, for when placed

under favorable conditions of temperature development proceeds normally, no matter at what stage of the dormant period the collection is made. On the other hand, the buds of Assiniboine collected before the middle of January are so deeply dormant that under the same conditions of temperature no visible change takes place and no blossoms are produced. Buds of Assiniboine, collected on January 24, bloomed 26 days later, on February 18. As this is the first visible response of these hardy buds, it is assumed to indicate the previous occurrence of some internal change which determines the breaking of the dormant condition. At this same

TABLE I

DEGREE OF DORMANCY OBTAINING IN HARDY AND SEMIHARDY BUDS AS MEASURED BY TIME REQUIRED FOR BLOOMING UNDER LABORATORY CONDITIONS AT DIFFERENT INTERVALS DURING SEASON OF DORMANCY

STELLA			TONKA			ASSINIBOINE		
Date of collection	Date of bloom	Time required for bloom	Date of collection	Date of bloom	Time required for bloom	Date of collection	Date of bloom	Time required for bloom
Oct. 3	Oct. 17	15	Oct. 3	Oct. 17	15	Oct. 3	....	......
Nov. 8	Nov. 22	15	Nov. 8	Nov. 22	15	Nov. 8	....	......
Nov. 19	Dec. 4	16	Nov. 19	Dec. 4	16	Nov. 19	....	......
Jan. 24	Feb. 2	10	Jan. 24	Feb. 2	10	Jan. 24	Feb. 18	26
Feb. 6	Feb. 15	10	Feb. 6	Feb. 15	10	Feb. 6	Feb. 23	18
Feb. 21	Mar. 2	11	Feb. 21	Mar. 2	11	Feb. 21	Mar. 8	17
Feb. 28	Mar. 7	9	Feb. 28	Mar. 7	9	Feb. 28	Mar. 14	16
Mar. 5	Mar. 13	9	Mar. 5	Mar. 13	9	Mar. 5	Mar. 19	15

time some change takes place also in the semihardy buds, for the period of development is shortened from 16 to 10 days. From January 24 throughout the remainder of the winter the degree of dormancy continues to decrease, and collections made on March 5 show that the length of time required for anthesis has been shortened to 9 days in the case of Stella and Tonka, and to 15 days in the case of Assiniboine. It must not be inferred that the time at which the break in dormancy occurs can be assigned to any particular day, for undoubtedly the changes involved proceed slowly, and development is initiated gradually. January 24 is emphasized as the time when the first evidence of a break in dormancy was observed, while in reality the changes involved may

extend through several weeks, taking place at a constantly accelerated rate as the season advances. It will be observed (figs. 1, 2) that the moisture content curve for Assiniboine shows some tendency

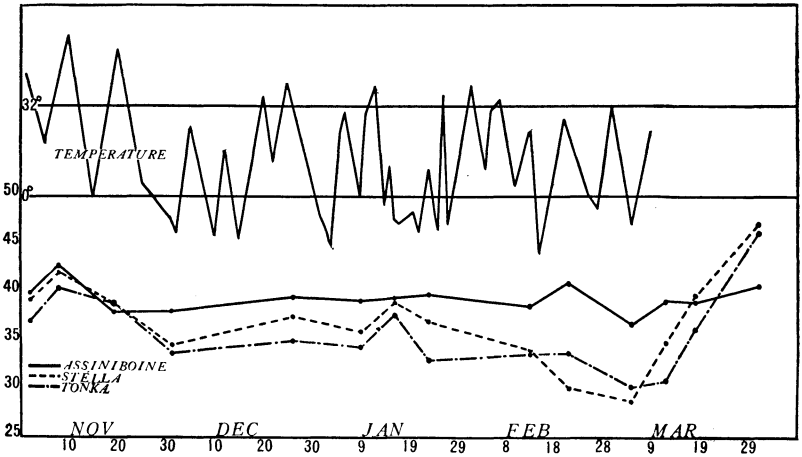

FIG. 1.—Moisture content fluctuations of leaf buds as related to temperature.

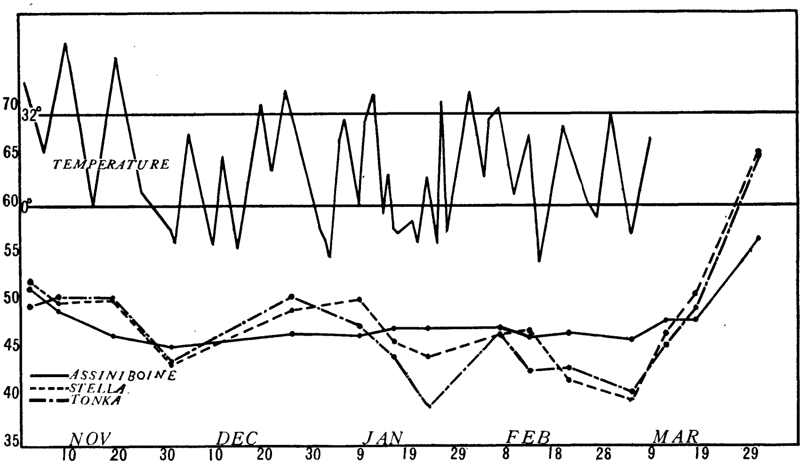

FIG. 2.—Moisture content fluctuations of fruit buds as related to temperature.

to become more irregular after January 25, and it may be that these fluctuations are due, in some measure at least, to internal changes incident to or causative of this break in dormancy. It is also significant to note here that the greatest injury to buds occurs

during the portion of the winter following this date, which marks an apparent (if not actual) break in dormancy (DORSEY and STRAUSBAUGH 5).

Moisture content and movement of water in hardy and semihardy buds

As in the break of dormancy, marked differences are also found in the moisture content of the hardy and semihardy buds. In both fruit and foliage buds of Assiniboine the moisture falls to a certain point early in the season, and then remains almost constant throughout the remainder of the winter up to the initiation of growth activity in the spring. In the buds of Stella and Tonka the moisture content undergoes some marked fluctuations during the course of the winter, and these coincide, in a general way at least, with corresponding fluctuations in temperature. The plotted

TABLE II

WATER LOSS FROM SEMIHARDY BUDS ACCOMPANYING MARKED LOWERING OF TEMPERATURES

Variety	Foliage buds			Fruit buds		
	November 19	December 1	Loss	November 19	December 1	Loss
Stella	39.08	34.68	4.40	50.38	43.51	6.87
Tonka	39.08	33.94	5.14	50.51	43.93	6.58
Assiniboine	38.12	38.30	....	46.51	45.49	1.02

curves show three distinct periods at which such a behavior in water movement in relation to temperature is indicated, namely, on December 1, January 23, and March 5. On November 30 the temperature fell to 8° F., and on December 1 the thermometer registered −12° F. Bud collections made at this time showed a decrease in moisture content as indicated in table II.

From the data of this table it will be noted that while the moisture content of the foliage buds decreased 4.4 per cent and 5.14 per cent respectively in Stella and Tonka, the foliage buds of Assiniboine showed practically no change. In the case of the fruit buds the loss in Stella and Tonka is 6.87 per cent and 6.58 per cent, while those of Assiniboine show the very slight loss of 1.02 per cent.

On January 21 the temperature again fell to -12° F. and remained approximately at zero through the following day. Bud collections were made on January 23. The losses in moisture at this time are set forth in table III.

TABLE III

WATER LOSS FROM SEMIHARDY BUDS AS COMPARED WITH HARDY BUDS LATER IN THE SEASON

Variety	Foliage buds			Fruit buds		
	January 16	January 23	Loss	January 16	January 23	Loss
Stella	39.23	37.17	2.06	45.98	44.34	1.64
Tonka	37.83	33.13	4.70	44.41	39.16	5.25
Assiniboine	39.61	39.95	....	47.36	47.31	0.05

In this instance it will be observed that the foliage buds in Stella and Tonka lose 2.06 per cent and 4.7 per cent respectively, while there is still practically no change in those of Assiniboine. Likewise the fruit buds in Stella and Tonka show a loss of 1.64 per cent and 5.25 per cent, while Assiniboine fruit buds show the almost inappreciable loss of 0.05 per cent. Again, on March 4, the temperature fell to 0° F. and on March 5 to -9° F. Bud collections made on March 5 showed losses in moisture content, as given in table IV.

TABLE IV

WATER LOSS FROM BUDS ACCOMPANYING MARKED LOWERING OF TEMPERATURE STILL LATER IN THE SEASON

Variety	Foliage buds			Fruit buds		
	February 21	March 5	Loss	February 21	March 5	Loss
Stella	30.25	28.87	1.38	41.98	39.78	2.20
Tonka	33.82	30.22	3.60	43.24	40.46	2.78
Assiniboine	41.20	36.87	4.33	46.83	46.16	0.67

On this date the moisture content of foliage buds in Stella decreased 1.38 per cent and in Tonka 3.6 per cent. The foliage buds of Assiniboine here show a loss of 4.33 per cent, which is not in accord with the data shown in tables II and III. This high percentage, however, is undoubtedly due to some error in the determination of moisture content for February 21, the value

(41.20 per cent) obtained on this date being too high to agree with the general results of the other determinations. The fruit buds of Stella and Tonka show losses of 2.2 per cent and 2.78 per cent, while those of Assiniboine show a loss of only 0.67 per cent. The changes in moisture content as shown in tables III and IV are not so great as those observed in table II. The curves (figs. 1, 2) show this relation much more clearly. It would have been interesting, for the sake of comparison, to have made determinations on February 15, when the lowest temperature of the winter was reached, but unfortunately no collections were made between February 13 and February 21.

TABLE V

INCREASE IN WATER CONTENT OF SEMIHARDY BUDS ACCOMPANYING MARKED RISE IN TEMPERATURE

Variety	Foliage buds			Fruit buds		
	December 1	December 26	Increase	December 1	December 26	Increase
Stella	34.68	37.6	2.92	43.51	49.3	5.79
Tonka	33.94	35.2	1.26	43.93	50.7	6.77
Assiniboine	38.30	39.7	1.40	45.94	46.80	0.86

It will now be interesting to note what effect a marked rise in temperature will have upon the water content. The temperature from December 20 to December 26 was relatively high, ranging well over 20° throughout this time and reaching a maximum of 40°. Bud collection made on December 25 showed a moisture content as given in table V. In this table it appears that the moisture content under certain conditions may increase with rise in temperature. Foliage buds of Stella showed an increase of 2.92 per cent, those of Tonka 1.26 per cent, while those of Assiniboine showed an increase of 1.4 per cent. In comparison with the foliage buds, the fruit buds of Stella and Tonka increased their moisture content 5.79 per cent and 6.77 per cent respectively; and in contrast the fruit buds of Assiniboine showed a strikingly slight increase of only 0.86 per cent. Thus it seems evident that the movement of water in the semihardy twigs and buds is easily influenced by fluctuations in temperature, but the response in

hardy buds to the same conditions is more tardy and much less pronounced. In March when the buds begin to swell the moisture content increases very rapidly, as is shown in table VI.

Table VI shows clearly the slower movement of water in the hardy form, for while the moisture content in the foliage buds of the semihardy varieties increased 18.41 per cent and 16.05 per cent, that of the hardy Assiniboine increased only 3.83 per cent. In the fruit buds of Stella and Tonka the increase was 25.8 per cent and 24.91 per cent, while that of Assiniboine was only 10.36 per cent. It will be seen that marked and well defined changes take place in the water content of buds under different sets of conditions.

TABLE VI

INCREASE IN WATER CONTENT WHEN BUDS ARE RESUMING GROWTH ACTIVITY IN SPRING

Variety	Foliage buds			Fruit buds		
	March 5	March 31	Increase	March 5	March 31	Increase
Stella	28.87	47.28	18.41	39.78	65.58	25.80
Tonka	30.22	46.27	16.05	40.46	65.37	24.91
Assiniboine	36.87	40.70	3.83	46.16	56.52	10.36

TABLE VII

SUMMARY OF DATA ON MOISTURE CONTENT OF LEAF AND FRUIT BUDS FOR NOVEMBER 8 TO MARCH 31

Date	Tonka		Stella		Assiniboine	
	Leaf bud	Fruit bud	Leaf bud	Fruit bud	Leaf bud	Fruit bud
November 8	40.57	50.64	42.34	50.01	43.15	49.38
November 19	39.08	50.51	39.08	50.38	38.12	46.51
December 1	33.94	43.93	34.68	43.51	38.30	45.49
December 26	35.2	50.7	37.6	49.3	39.7	46.8
January 9	34.4	47.5	36.0	50.3	39.03	46.6
January 16	37.83	44.41	39.23	45.98	39.61	47.36
January 23	33.13	39.16	37.17	44.34	39.95	47.31
February 6	....	46.55(?)	34.29	46.54	....	47.43
February 13	33.74	42.89	34.14	47.17	38.64	46.44
February 21	33.82	43.24	30.25	41.98	41.20	46.83
March 6	30.22	40.46	28.87	39.78	36.87	46.16
March 12	30.83	45.51	34.83	46.75	39.37	48.12
March 18	36.20	49.43	39.71	50.93	39.03	48.04
March 31	46.27	65.37	47.28	65.58	40.70	56.52

These changes appear conspicuously when the data for the entire dormant season are presented.

An examination of the data of Table VII reveals three very significant facts. First it will be noticed that throughout the period of dormancy the moisture content of the leaf buds of a given variety is considerably lower than that of the fruit buds. This may be a factor in the greater resistance of the leaf buds to low temperatures. In the second place it will be observed that the moisture content of the leaf buds of Assiniboine is uniformly higher than that of the leaf buds of the other two varieties. Lastly the moisture content of the fruit buds of Assiniboine is lower or higher than that of the fruit buds of Stella and Tonka according to the temperatures prevailing at the time the collections are made.

Dehydration of buds by sulphuric acid

When the marked differences in moisture content and moisture retention of leaf and fruit buds in these varieties with different degrees of hardiness became apparent, it seemed advisable to investigate such differences further. Accordingly a series of experiments was undertaken, first with buds alone, and later with buds attached to the twigs, to study the movement of moisture by carefully controlled laboratory methods. Fruit buds were collected in small weighing dishes provided with closely fitting covers. These dishes were then placed uncovered in sealed chambers containing different concentrations of sulphuric acid. The buds were weighed before being placed in the chambers, and subsequently at intervals of 12–48 hours, to determine the water loss. When the weighings were being made the lids were placed on the dishes while they were out of the chambers.

The results of the experiment with buds alone were not entirely satisfactory, and consequently it was repeated with one very essential modification, namely, the fruit and flower buds were not detached from the twigs. In the repetition experiment entire twigs 10–12 inches in length, with buds attached, were removed from the tree and placed in sealed chambers so that the twig-bud system as a unit was exposed to the air inclosed over different concentrations of sulphuric acid. In determining the moisture losses

weighings were made as before. The desiccators in these experiments were kept in a refrigeration room where the temperature remained quite constant at about 34° F. This low temperature

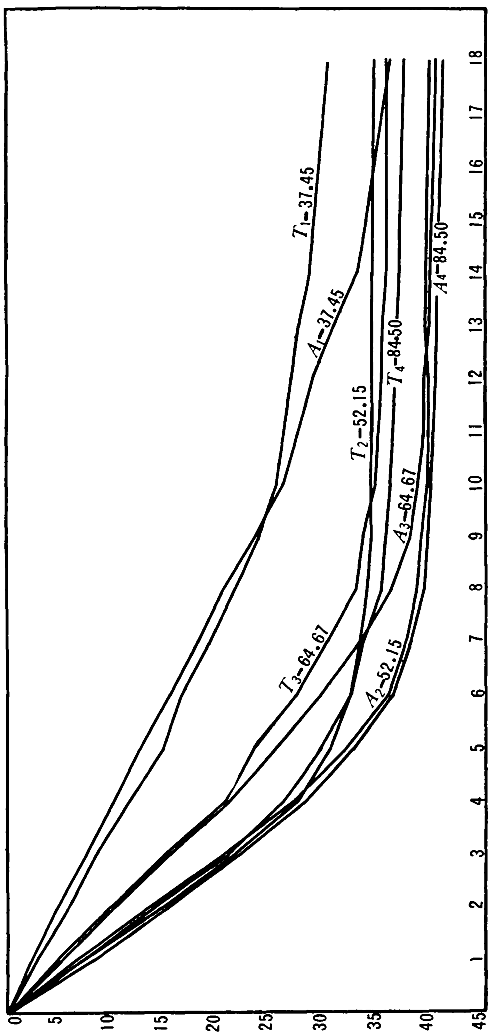

FIG. 3.—Loss of moisture from detached buds exposed to an atmosphere inclosed over sulphuric acid of different concentrations; *A*, Assiniboine; *T*, Tonka; numbers indicate concentration of acids; *C*, distilled water check.

was chosen as a precautionary measure against the possibility of the occurrence of any growth changes. Fig. 3 shows that the loss is almost uniform in both hardy and semihardy buds in every case

except those in which the more dilute acids were used. Since this uniformity of water movement in both hardy and semihardy buds was not in accord with the behavior of the buds under normal conditions, it was thought that it might be due to the escape of

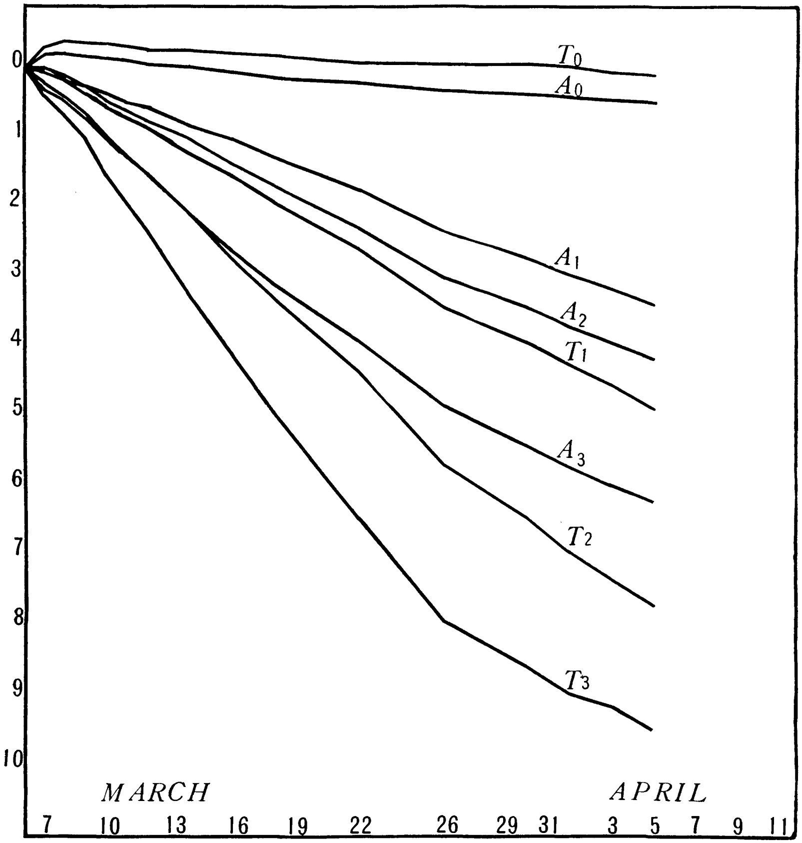

FIG. 4.—Loss of moisture from twigs with buds attached when exposed to atmosphere inclosed over sulphuric acid of different concentrations; *A*, Assiniboine; *T*, Tonka; concentrations of acid as follows: (1) 24.12 per cent, (2) 37.45 per cent, and (3) 84.50 per cent; *C*, distilled water check.

moisture through the wound surface made in severing the buds from the twigs. To test this assumption a collection of twigs with the buds in place was introduced into the sealed chambers and weighed at regular intervals of 24–48 hours. The cut ends of the

twigs were sealed with paraffin immediately after they were removed from the tree, so that all escape of water from the tissues must have taken place in a manner similar to that which occurs under normal conditions when the twigs remain on the tree. Fig. 4 and table VIII show the results of this experiment.

TABLE VIII

PERCENTAGE OF MOISTURE LOST FROM TWIGS OF TONKA AND ASSINIBOINE WHEN EXPOSED TO AN ATMOSPHERE OVER DIFFERENT CONCENTRATIONS OF SULPHURIC ACID FOR 28 DAYS

Variety	Percentage loss over distilled water	Percentage loss over H_2SO_4 (24.12%)	Percentage loss over H_2SO_4 (37.45%)	Percentage loss over H_2SO_4 (84.50%)
Tonka....................	0.04	4.83	7.7	9.49
Assiniboine...............	0.48	3.38	4.17	6.2

It will be noted that the water loss from the semihardy twigs is much greater than from the hardy twigs. With the highest concentration of acid used, the loss from the semihardy twigs is nearly 9.5 per cent, while that from the hardy twigs is slightly over 6 per cent. This tardiness in water movement is in full agreement with that occurring in the twigs under normal conditions as shown in the graphs of the moisture content curves. It will also be observed (fig. 4) that the twigs exposed to a saturated atmosphere over distilled water absorbed less than 0.5 per cent of moisture. This fact would seem to counter the claims of some workers to the effect that there is a considerable exchange of moisture between the tissues and the air, and to establish beyond doubt that the moisture content of the twigs does not increase markedly with an increase in atmospheric humidity.

In order to determine the relative amounts of moisture given off from the twigs to the air through evaporation caused by winds, twigs of four varieties, including hardy and semihardy forms, were removed from the trees and the cut ends immediately sealed with paraffin. These twigs were then supported upright in Petri dishes by means of paraffin, and after being weighed were placed in a strong current of air produced by two large electric fans. The dishes containing the twigs were weighed daily, and at the end of

three days the loss in all cases was found to be practically negligible, the greatest loss being only 0.7 gm. from a total weight of 137.47 gm., or a little more than 0.5 per cent. Thus it seems quite evident that there is little exchange of moisture between the air and the tissues of the twigs due to evaporation alone, but that some dehydrating force is necessary to account for such losses as have been shown to take place in connection with low temperatures.

In the studies of water loss from twigs in the acid chambers and also by the fan method, a conspicuous structural difference in the bark of the hardy form as compared with that of semihardy forms became evident. This difference may possibly be associated in some way with the slower movement of water in the hardy variety. The twigs in all three of the forms studied are covered with a heavy suberized layer which renders them impervious to water except through the lenticels. The number of these lenticels per unit surface is fairly constant for a given variety, but a marked difference is observed between hardy and semihardy varieties. Five separate counts were made on sections of twigs of Stella and Assiniboine. The sections chosen were 5 cm. long and 1.2 cm. in diameter, representing in each case a curved surface area of 18.85 sq. cm. Table IX gives the result of these counts.

TABLE IX

NUMBER OF LENTICELS PRESENT ON 18.85 SQ. CM. OF TWIG SURFACE

Stella	Assiniboine
49	12
54	10
48	8
39	13
54	11

As these lenticels are approximately the same size in each variety, it will be seen that the total lenticel area in the semihardy form is from 3 to 6 times that occurring in the hardy variety. The exact significance of this marked difference in bark character is not fully clear, but that it may be related in some way to the more tardy movement of water from the twigs of Assiniboine is a possibility that seems worthy of consideration.

Discussion

In recent years the horticulturists of the northern United States and Canada have been greatly interested in the breeding of hardy fruits capable of resisting the low temperatures of this latitude. One of the difficulties met with in this work has been the amount of time required to test new seedlings for hardiness. Various attempts have been made to discover some means of detecting hardiness by direct observation at an early period in the development of the seedling.

BEACH and ALLEN (3) made a rather extensive series of microscopical, mechanical, and specific gravity tests of apple twigs to ascertain whether "the hardiness of a tree could be determined while it was still in the nursery." They concluded that "from the practical point of view as yet it is impossible to name any one test by which the degree of constitutional hardiness of a seedling apple may be foretold." This work, however, has revealed some very interesting and suggestive facts that may have a fundamental value in the physiological study of hardiness. Among other things they found that "the hardier varieties on the average had a slightly lower moisture content than the more tender varieties," and that "this difference is more marked during the growing season." They state that this "difference in water content can be explained partly at least by the fact that the more tender sorts evaporate water more rapidly than do the hardy varieties. Freezing tends to dry the twig out, and after a period of very cold weather the twigs of the hardy varieties are generally found to contain the most moisture."

JOHNSTON (7) found that "as the season advances the difference between the water content of fruit buds of the Elberta and Greensboro peach becomes more marked, the values for the Elberta being the greater." Since the Greensboro peach is considered more hardy than the Elberta, the inference is that the more tender buds have the highest moisture content. In these determinations only 10 buds were used in a sample, and it would seem that larger amounts of the tissue might give more reliable results.

SHUTT (11) found the moisture content of apple twigs of tender varieties higher than that of hardy twigs. He stated "that we have

direct and definite proof that there is distinct relationship between the moisture content of the twig and its power to resist the action of frost, and that those trees whose new growth contains the largest percentage of water as winter approaches are in all probability the most tender." He also believes that hardiness is a quality that can be affected by cultural methods. He says that "hardiness is evidently something more than an inherited tendency. It seems probable that it is a quality largely under the influence of the soil conditions as regards moisture and temperature in the late summer and autumn months, and probably these factors rather than the severity of the succeeding winter determine the tree's immunity from frost. If in northern latitudes vegetative growth be early arrested and ripening of the new wood thus induced, either by artificial means (pruning and cover crops) or by a dry and cold autumn, varieties now considered tender might prove hardy."

There can be no doubt as to the effect of cultural methods upon the ability of certain plants to withstand low temperatures. This effect is shown by the work of BATCHELOR and REED (2), who found that one of the factors in the winter injury of the Persian walnut (*Juglans regia*) was winter drought. The injury referred to is a killing of the distal ends of the branches rather than that of the buds alone. Under certain conditions they were able to prevent winter injury by irrigating heavily late in the season, after maturation had been induced by withholding the water supply during the latter part of the summer. Their work shows a very evident relation between soil moisture and winter injury.

In the introduction attention was called to the fact that dormancy occurs in widely varying degrees. The range extends from no dormancy at all to profound dormancy, with every degree of intergrading conditions. If in perennial woody plants there is a positive correlation between dormancy and hardiness, it follows that there must be a corresponding range of hardy conditions. If the forms under consideration chance to be closely related as to position in the series, or closely adjusted to the equilibrium of the external environment, it is easily conceivable that cultural methods may affect the relative degree of hardiness within certain limits. Such a case would seem to be exemplified by the Persian walnut

grown under California conditions. On the other hand, it must be admitted that other factors are operating when we have to deal with forms whose requirements lie well within the limits of physical environment, or with forms widely separated in respect to the degree of hardiness they possess. It is difficult to conceive of any modification of external conditions that could induce a degree of hardiness in Tonka and Stella which would even approach the hardy condition that obtains in Assiniboine. The fact should be kept in mind, however, that Assiniboine belongs to a different species from Stella and Tonka, and also that what is true of the apple need not of necessity be true of the plum or the peach.

The investigations show a higher moisture content for tender apple twigs and tender peach buds than that of the hardier forms. In the plum, however, at least during the period of dormancy, it is not the relative amount of water present in the buds, but the relative water-retaining capacity that constitutes a distinct difference between hardy and semihardy forms. In the apple, BEACH and ALLEN found that the greater moisture content of the tender twigs as compared with hardy twigs was much more pronounced during the growing season. Whether such a relation obtains between hardy and tender varieties of the plum during the period of vegetative activity has not yet been determined. It may easily be possible that the problem of hardiness will require specific investigation for each species in question, and that as yet no very far reaching generalizations on the subject can be made.

In the case of the plum, microchemical studies (5) indicate that the dormant condition of the buds involves a protoplasmic change of some sort which is much more marked in the buds of the hardy variety. There is an evident modification in the proteins of the buds, but practically nothing is known at present concerning the nature of this change. It is possible that there is induced as a result of these modifications a very decided change in the colloidal condition within the cells which increases the force of imbibition, so that the water of the protoplast is retained against the dehydrating force of freezing, and the protoplasm is not disorganized. There is no evidence that the hardy buds contain less moisture than the tender buds during the dormant period; in fact, when the temperature drops very low the hardy buds contain the most water

(figs. 1, 2 and table VII). The point that must be emphasized, however, is that the hardy buds have the capacity to retain their moisture at a certain definite and fairly constant minimum throughout the period of dormancy regardless of all fluctuations in temperature, and that this capacity is not a characteristic of the semihardy or tender buds. WIEGAND (12) states as follows:

> Every cell has its critical point, the withdrawal of water beyond which will cause the death of the cell, whether by ordinary evaporation or by other means. It may be supposed that the delicate structure of the protoplasm necessary to constitute living matter can no longer sustain itself when too many molecules of water are removed from its support. In the great majority of plants this point lies so high in the water content that it is passed very soon after the inception of ice formation, hence the death of so many plants at this period. Others may be able to exist with so little water that a very low temperature is necessary before a sufficient quantity is abstracted to cause death. From some plants enough water cannot be extracted by cold to kill them.

The hardy plum, Assiniboine, lies very close to the last mentioned class of plants. It requires exceedingly low temperatures to cause it injury, and the explanation of this fact seems to lie in its ability to retain its moisture. Water movement in its tissues seems to be much slower, so that it matures earlier in the autumn and assumes its maximum water content more slowly in the spring. The fact that it blooms from two to three days earlier than the semihardy varieties may be due to the possibility of growth activities taking place with a much lower water content.

The moisture relations that obtain between the hardy and semihardy buds of the plum indicate a wide difference in their physiological reactions. These reactions arise from specific conditions within the cells, and therefore it is assumed that the protoplasmic structure of the hardy tissues is different from that of the semihardy tissues. These differences are inherent, so that they furnish a basis for the work of the plant breeder. There is a suggestion here, therefore, that a study of the moisture relations of seedling plants during both the dormant and vegetative conditions may afford a tentative basis for determining selections.

Summary

1. In the plum there are widely differing degrees of dormancy among the different species and varieties. There appears to be a

definite relation between dormancy and hardiness. Assiniboine is extremely hardy and its dormancy is very profound, in contrast with Tonka and Stella, two semihardy varieties in Minnesota, which appear to enter real dormancy for only a very short period in early winter, if they do so at all.

2. During the period of dormancy the moisture content of the semihardy varieties fluctuates with the temperature. Periods of low temperatures are accompanied by a loss of moisture from the leaf and fruit buds, and higher winter temperatures, which are seldom above freezing in Minnesota, by an increase in moisture content. In comparison with the semihardy varieties the moisture content of Assiniboine remains at a definite and fairly constant minimum throughout dormancy.

3. When the fluctuations in the moisture content of buds were found to occur under orchard conditions, this phase of the problem was checked under control in the laboratory by placing the twig-bud-system in sealed chambers over different concentrations of sulphuric acid. By this method water movement in the tissues of Assiniboine was found to take place more slowly than in Stella and Tonka. Lenticel number per unit area was found to be correlated with the difference in moisture retaining capacity.

4. Somewhere near the mid-point of the dormant period fundamental metabolic changes occur which affect the ecological reactions of apparently dormant plum trees in a striking manner. As a result of these changes, or at least coincident with them, winter killing in the flower buds is found for the first time, the moisture retaining capacity of the fruit and leaf buds is changed, and anthesis occurs when fruit buds are subjected to favorable growth temperatures in the greenhouse. These changes are interpreted as indicating the time when the rest period is broken.

5. The dormant condition reached by the hardy forms, such as Assiniboine, appears to involve fundamental protoplasmic changes. Among these there may be a change in colloidal properties creating an increased imbibition which may account for the marked retention of water against the force of dehydration.

6. This investigation has a direct bearing upon the applied problem of selecting seedling fruits for hardiness. A study of the

moisture relations in forms differing in hardiness may furnish the fruit breeder with a criterion, correlated with hardiness, which will hasten markedly the final selections.

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